

Skull of Early Eocene *Cantius abditus* (Primates: Adapiformes) and Its Phylogenetic Implications, With a Reevaluation of “*Hesperolemur*” *actius*

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ABSTRACT A substantially complete skull and mandible of the primitive adapiform *Cantius* is reported from the Early Eocene Willwood Formation of Wyoming. The mandible contains an almost complete lower dentition in which the lower incisors are strongly inclined and have spatulate crowns, I_2 is larger than I_1 , and the canine is large and projecting. The cranium shares many features with those of *Notharctus* and *Smilodectes* but differs in having nasals that broaden proximally. Presence of a prominent canine and strong sagittal crest may indicate that it represents a male. The basicranium preserves auditory structures almost identical to those in extant noncheiropithecoid lemurs, including a large bony tube for the stapedia artery and a small, open sulcus for the distal portion of the promontorial artery.

The dentition is sufficiently primitive to be compatible with a relationship to either strepsirrhines or anthropoids, but the anatomy of the auditory region is more consistent with either specific relationship to lemurs or, more likely, a basal position that approximates the euprimate morphotype.

Certain features of the basicranium of “*Hesperolemur*” *actius*, described by Gunnell ([1995] Am. J. Phys. Anthropol. 98:447–470) as being unlike that of any other adapiform, were either misinterpreted or are apparently no longer present in the holotype. Reassessment of these and other features indicates that in fact “*H.*” *actius* differs little from *Cantius* and should not be separated from the latter at the genus level, although on dental grounds the species appears to be distinct (as *C. actius*). Am J Phys Anthropol 109:523–539, 1999. © 1999 Wiley-Liss, Inc.

The Early Eocene notharctid *Cantius* is one of the oldest and most primitive known euprimates, lying near the base of the adapiform primate radiation (e.g., Gingerich, 1986; Rose, 1995b; Rose et al., 1994). In body size and overall anatomy, *Cantius* resembled extant lemurs such as *Lepilemur*, and was probably an active arboreal quadruped (Rose and Walker, 1985). Although adapiforms are represented by some of the best-preserved

material known for any fossil primates, their precise relationship to extant primates remains controversial. They are variously con-

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sidered to be the sister group of living strepsirrhines (e.g., Kay et al., 1997) or of anthropoids (e.g., Simons, 1995; Simons and Rasmussen, 1996), although some of the similarities to both groups could be primitive euprimate traits.

A common Wasatchian mammal in western North America (less frequently known from Europe), *Cantius* is best known from the Willwood Formation of the Bighorn Basin, Wyoming, where it typically accounts for about 10% of the mammalian fauna at rich localities (Gingerich and Simons, 1977; Bown, 1979; Rose, 1981; O'Leary, 1996). Thousands of specimens of *Cantius* have been found in the Bighorn Basin, but nearly all are jaw fragments and teeth. Despite more than a century of field work there, only a small number of referable snouts have been found, and the skull of this basal adapiform has remained elusive.

The impetus for this study was the discovery of a substantially complete skull and mandible of *Cantius abditus* in July 1993, by a joint Johns Hopkins-U.S. Geological Survey field party working in the Early Eocene (Wasatchian) Willwood Formation of the Bighorn Basin. USNM 494881 is the oldest known skull of any adapiform primate, and its dentition and basicranium are more complete than those of any other known specimen of *Cantius*. The combination of its antiquity, completeness, and basal phylogenetic position make this a particularly important specimen for documenting craniodental character states in primitive adapiforms, and their implications for higher-level relationships of adapiforms.

In the course of this study, comparisons were made with other notharctids for which skulls are known: the Bridgerian notharctids *Notharctus* and *Smilodectes*, both known from several complete skulls (e.g., Gregory, 1920; Gazin, 1958; Alexander, 1992a,b, 1994), and the recently described holotype skull of "*Hesperolemur*" *actius* (Gunnell, 1995). The last-named specimen turned out to be of considerable interest, as our interpretation of its basicranial anatomy differs significantly from the one presented in the original study.

Institutional abbreviations used are as follows: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; MPM, Milwaukee Public Museum, Milwaukee, Wisconsin; SDSNH, San Diego Society of Natural History, San Diego, California; USGS, U.S. Geological Survey, Denver, now housed at USNM; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

MATERIALS AND METHODS

The principal focus of this study is a skull and mandible of *Cantius abditus*, USNM 494881 (formerly USGS 38493), from USGS locality D-2003 in the southern Bighorn Basin of Wyoming. The productive paleosol at this site is situated at 479 m in the Willwood Formation (Wasatchian, Wa-6 zone, early "Lysitean"). This is relatively high in the formation and about 2 million years younger than the oldest and most primitive fossils of *Cantius*, which come from the earliest Wasatchian (Wa-0 zone; Gingerich, 1989; Wing et al., 1991). *C. abditus* is one of the latest-occurring and dentally most derived species of the genus. Interspecific dental differences relate primarily to the molars, however, and there is no evidence to suggest that the earliest *Cantius* species were significantly different from *C. abditus* in basicranial anatomy or anterior dental configuration.

AMNH 88801 and 88802, petrosals referred to *Cantius ralstoni* from the early Wasatchian Four Mile local fauna (East Alheit Quarry) of Colorado, also provided information on the auditory region. Additional data on the snout came from AMNH 15017, the holotype of *C. trigonodus*, reconstructed by J.P.A.

Comparisons were made to numerous specimens of *Notharctus* (including AMNH 11466, 11480, 127167, 129382, 131764, and 131776), *Cantius* (AMNH 14656 and 55157), and *Smilodectes* (UM 32773 [=MPM 2612], USNM 21815, and AMNH 131762).

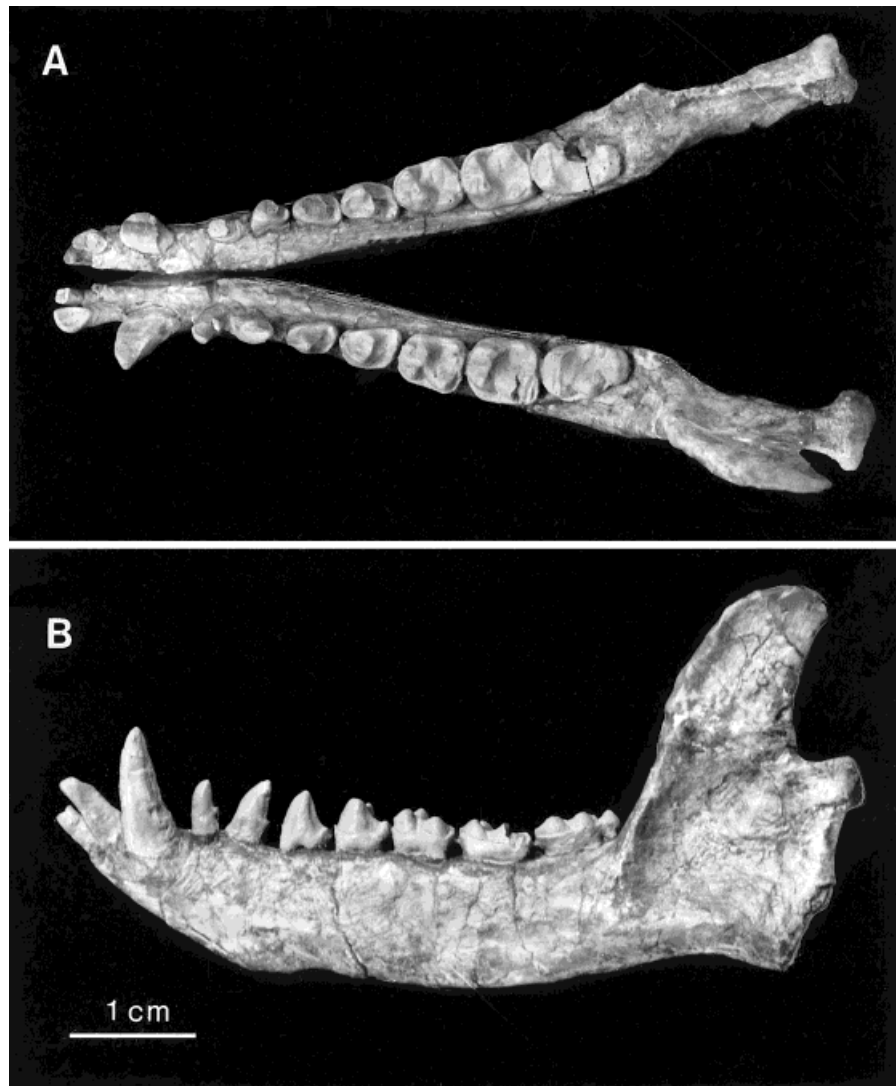


Fig. 1. Occlusal (A) and lateral (B) views of mandible of *Cantius abditus*, USNM 494881.

SDSNH 35233, the holotype of *Hesperolemur actius*, was reexamined and compared to *Cantius*.

COMPARATIVE ANATOMY

Mandible and lower dentition

Description. The mandible of USNM 494881 (Fig. 1) is the most nearly complete known lower jaw of *Cantius*. (See Table 1 for abbreviations in figures.) The coronoid process and condyle are essentially intact on

the left side, but the angular processes are incomplete on both sides. The corpus of the mandible is shallow and of consistent depth below the lower tooth row; it does not deepen below the symphysis, despite the presence of prominent canines. In some probably male *Notharctus* specimens (e.g., AMNH 11480 and 127167), the mandible is deeper at the symphysis, whereas others (e.g., AMNH 131764) have a uniformly shallower jaw. The mandibular symphysis in USNM 494881

TABLE 1. Abbreviations used in figures

ant. sept.	Anterior septum
art.	Artery
Boc.	Basioccipital bone
Bsp.	Basisphenoid bone
bull.	Auditory bulla
coch. can.	Cochlear canaliculus
cr.	Crest
epitym. rec.	Epitympanic recess
fac. can.	Facial canal
fen. coch.	Fenestra cochleae
fen. vest.	Fenestra vestibuli
for. mag.	Foramen magnum
fos. tens. tym.	Fossa for tensor tympani muscle
glen. fos.	Glenoid (mandibular) fossa
int. car. can.	Internal carotid canal
jug. for.	Jugular foramen
nuch. cr.	Nuchal crest
occ. con.	Occipital condyle
postglen. for.	Postglenoid foramen
postglen. proc.	Postglenoid process
prom.	Promontorium (cochlear housing)
prom. art.	Promontorial artery
sag. cr.	Sagittal crest
sept.	Septum
spir. lam.	Osseous spiral lamina
stap. can.	Stapedial canal
stylo. for.	Stylomastoid foramen
sulc.	Sulcus
tub. can.	Tubal canal (for auditory tube)

TABLE 2. Selected measurements (mm) of *Cantius abditus*, USNM 49488¹

Tooth	Length	Maximum breadth	Breadth trig.	Breadth tal.
I ₁	1.70 ²	1.30 ²		
I ₂	2.75	2.00		
C ₁	4.15	3.00		
P ₁	2.00	1.80		
P ₂	3.00	1.85		
P ₃	4.05	2.50		
P ₄	4.40		3.15	2.85
M ₁	4.40		3.90	4.15
M ₂	5.50		4.40	4.70
M ₃	7.10		4.15	4.15
C ¹	5.20	3.30		
P ¹	2.00R	1.75R		
P ²	3.00R	2.00R		
P ³	3.45	4.10		
P ⁴	4.20	5.45		
M ¹	5.25	7.60		
M ²	5.55R	7.75		
M ³	4.20	6.25		
I ₂ crown height (enamel base to crown tip)				3.50
C ₁ crown height				10.00
Mandibular depth, buccal below RM ₁				9.70
Foramen magnum breadth				10.95
Foramen magnum height				8.55

¹ R, measurements of right side; all others are of left side. All lengths are mesiodistal; breadths are buccolingual.

² Measurements taken on broken crown.

extends back to a position below P₂ and is unfused, in contrast to *Notharctus*. The coronoid process is high and well-developed, and the condyle is elevated well above the tooth row.

On the medial aspect of the mandibular angle there is a strong ridge parallel to the lower border of the dentary and running forward almost to the mandibular foramen; it is probably related to attachment of the medial pterygoid muscle. Such a ridge also occurs in *Notharctus* and *Pelycodus jarrovi* (AMNH 55514). In the latter, the mandibular angle is short, extending only 3 mm beyond the posterior border of the ascending ramus. The angle in *Cantius abditus* (USNM 494881) is incomplete but closely resembles that of *P. jarrovi*. Both descend below the inferior margin of the dentary and are slightly infected medially. This contrasts with *Notharctus tenebrosus* (AMNH 127167) and *Smilodectes gracilis* (AMNH 131762), in which the mandibular angle accounts for about 15% of the dentary length. The medially recurved angles of these taxa are greatly expanded inferior to the medial ridge and expand into an additional ridge on their inferior borders. *Cantius abditus* and

P. jarrovi probably exhibit the primitive condition of the mandibular angle for North American adapiforms.

The lower left dentition of USNM 494881 is complete except for the crown of I₁, while the right side contains P₂–M₃ and the roots and crown bases of I₁₋₂, C, and P₁ (see Table 2 for measurements). The one-rooted P₁ and two-rooted P₂ are simple, tall, and pointed, and are separated from each other and adjacent teeth by short diastemata. Aside from the most anterior teeth, the dentition of *C. abditus* is well-known (e.g., Gingerich and Simons, 1977; O'Leary, 1996) and needs no further discussion.

Perhaps the most striking feature of the preserved dentition is the lower incisor configuration, which has previously been unknown in *Cantius*. Although adapiforms are commonly said to have vertically implanted incisors, those of *Cantius abditus* (both roots and crowns) are strongly inclined at an angle of about 45°, much more so than in *Adapis parisiensis* (Gingerich, 1975, 1981) and more than in most specimens of *Notharctus*. In fact, there is considerable variation in degree of procumbency of notharctid inci-

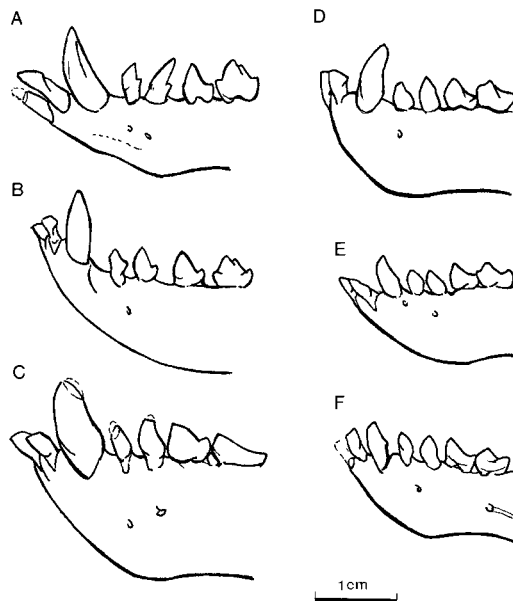


Fig. 2. Left dentaries of notharctid species displaying variable orientation of incisors. **A:** *Cantius abditus*, USNM 494881. **B:** *Cantius nunienus*, AMNH 55157. **C:** *Notharctus rostratum*, AMNH 11480. **D:** *Notharctus tenebrosus*, AMNH 131776 (male). **E:** *Notharctus tenebrosus*, AMNH 129382 (female, reversed). **F:** *Smilodectes gracilis*, USNM 21815 (reversed).

sors (Fig. 2). AMNH 55157 and 131776, for example, have almost vertical incisors, whereas YPM 12956 (*Notharctus tenebrosus*; Fig. 1 in Rosenberger et al., 1985) and AMNH 129382 have incisors almost as inclined as in *C. abditus*; but we have not seen any *Notharctus* specimen with more procumbent incisors than in *C. abditus*.

I_2 is clearly larger than I_1 , and its crown is broad and spatulate (although the roots of both incisors are laterally compressed), and somewhat asymmetric, as in *Notharctus* and *A. parisiensis*. The lingual aspect of I_2 is gently concave, with a low longitudinal ridge of enamel situated near the midline of the this surface, a feature not observed in I_2 of *Notharctus tenebrosus* (AMNH 131764) or *Smilodectes gracilis* (AMNH 131762). There is a slight swelling on the I_2 of *Cantius nunienus* resembling the condition in *C. abditus*. The tip of the incisor in USNM 494881 shows only slight wear, and not the heavy wear seen on the incisor tips of the specimens of *N. tenebrosus* and *S. gracilis*,

despite comparable molar wear. A probable left I_1 is preserved in another specimen of *Cantius* (USGS 25244); it is slightly smaller but otherwise similar to I_2 in USNM 494881.

Differences in canine size, skull size, and expression of sagittal and nuchal crests have been cited as evidence that some adapiforms were sexually dimorphic (e.g., Gingerich, 1981, 1995; Krishtalka et al., 1990; Alexander, 1994; Simons et al., 1995). The canines of USNM 494881 are large and trenchant and lack any indication of a mesial cristid (Greenfield, 1995), suggesting that it almost certainly represents a male. They are strongly convex labially but nearly flat lingually, with a low lingual cingulum. The canines project almost vertically and do not form a functional unit with the incisors as they do in *Adapis parisiensis* (Gingerich, 1975).

Discussion. Although the procumbency of the incisors of *Cantius* is consistent with the hypothesis that notharctids more closely approach the inferred pretooth-comb state for strepsirrhines than do adapids, these teeth cannot be described as being narrow and elongate as in tooth-combed prosimians. Moreover, as just noted, the canines are neither procumbent nor incisiform, in contrast to tooth-combed prosimians.

The anterior teeth of *Cantius* more closely approach those of primitive anthropoids such as *Catopithecus* (Simons, 1995) in relative proportions and crown morphology, but the incisors are more inclined. Kay et al. (1997) questioned the significance of the adapoid-anthropoid incisor resemblance on the basis that some omomyids have similar incisor proportions. While it is true that I_2 is slightly larger than I_1 in some omomyids (Covert and Williams, 1991), most omomyids had either subequal incisors or a much larger I_1 (Szalay, 1976; Gingerich, 1977; Bown and Rose, 1987; Rose, 1995a). Moreover, only one omomyid (*Macrotarsius*, i.e., the holotype of "*Hemiacodon jepseni*") is known to have had somewhat spatulate lower incisors, but they are less anthropoid-like than those of notharctids. Whether the resemblances of *Cantius* to anthropoids, including possible sexual dimorphism, imply a relationship (e.g., Gingerich, 1995; Greenfield, 1995; Simons, 1995)

or reflect symplesiomorphy or homoplasy (Kay et al., 1997) is debatable. Complicating the issue is the fact that the incisors of the putative Middle Eocene anthropoid *Eosimias* have pointed crowns and are wider basally than at the apex, rather than spatulate (Beard et al., 1996). Thus even the long-held notion that basal anthropoids had spatulate incisors is called into question.

USNM 494881 is the oldest adapiform for which we have the anterior dentition, and it is tempting to speculate that it displays the primitive anterior dental configuration for adapiforms. However, we still know little about the anterior dentition of the most primitive adapiform, *Donrussellia*. About all that can be said of the latter is that the canine was comparatively large and that the two known dentaries are shallow anteriorly (Godinot, 1981; Godinot et al., 1987), which suggests that the incisors were probably inclined and not significantly enlarged.

What, then, can be determined about the primitive anterior dental configuration of euprimates? The most primitive omomyids also had small incisors and a large canine (larger than the incisors but relatively smaller than in adapiforms), but the limited evidence available suggests that their incisor crowns were more pointed than spatulate. These incisors were slightly inclined to almost vertically implanted, and tended to be subequal in size, though several lineages evolved enlarged, more procumbent central incisors (Gingerich, 1977; Bown and Rose, 1987; Rose and Bown, 1991). The combined evidence from primitive adapids and omomyids, therefore, increasingly suggests that small, probably somewhat inclined incisors and a large canine were morphotypic for euprimates. *Cantius abditus* may approximate the primitive euprimate anterior dental configuration as closely as any known form. The polarity of spatulate crowns, however, a character shared with anthropoids, cannot be determined at present.

Skull

Description. Excluding the mandible, the skull of USNM 494881 is preserved in two pieces: the rostrum, broken at the postorbital constriction, and the braincase (Fig. 3). They do not meet perfectly, but very little is

missing. The skull is somewhat crushed and distorted, allowing few accurate measurements; nevertheless, several details of the snout, skull roof, and basicranium are discernible.

The ventral surface of the basioccipital is keeled, and the ventral surface of the basisphenoid is flat. The only known notharctid that deviates from this pattern is *Smilodectes gracilis*, which has the condition reversed (Alexander, 1993). The nasals, though poorly preserved, can be seen to flare proximally to form a broad, trapezoidal contact with the frontals and maxillae, similar to the condition in *Cantius trigonodus* (AMNH 15017), *C. nunienus* (AMNH 55157), and *C. venticolus* (AMNH 14656) (Alexander, 1992b, 1993, and in preparation).

The medial parts of the orbital region are present but badly distorted by crushing. The lacrimal foramen can be detected on both sides, but because of bone loss and deformation it cannot be determined whether the foramen was inside the orbit or on the face. A specimen of *Cantius abditus* illustrated by Gunnell (1995, Fig. 2) indicates that the foramen in this species opens on the face, just anterior to the orbital rim. In the adapids *Adapis*, *Leptadapis*, and *Pronycticebus* the lacrimal bone extends onto the face anterior to the orbit (Alexander, 1993); hence, this configuration appears to be primitive for adapiforms.

Apart from possibly sexually-dimorphic features, the braincase of *Cantius abditus* closely resembles those of *N. tenebrosus*, *S. gracilis*, and "*Hesperolemur*" *actius*. The dorsum of the skull exhibits a well-developed sagittal crest, like "*Hesperolemur*" and specimens of *Notharctus* that have been interpreted as males (Alexander, 1994). Known skulls of *Smilodectes* lack strong sagittal crests, suggesting that the sexual dimorphism of this character was minimal in this genus. Notharctids differ from *Adapis* and *Leptadapis* in having a shorter and lower sagittal crest, in which the temporal (frontal) lines converge behind, rather than at, the coronal suture. In *C. abditus* and other notharctids, the sagittal crest intersects the nuchal crest at a point projecting posteriorly over a broad, flattened occipital region. The

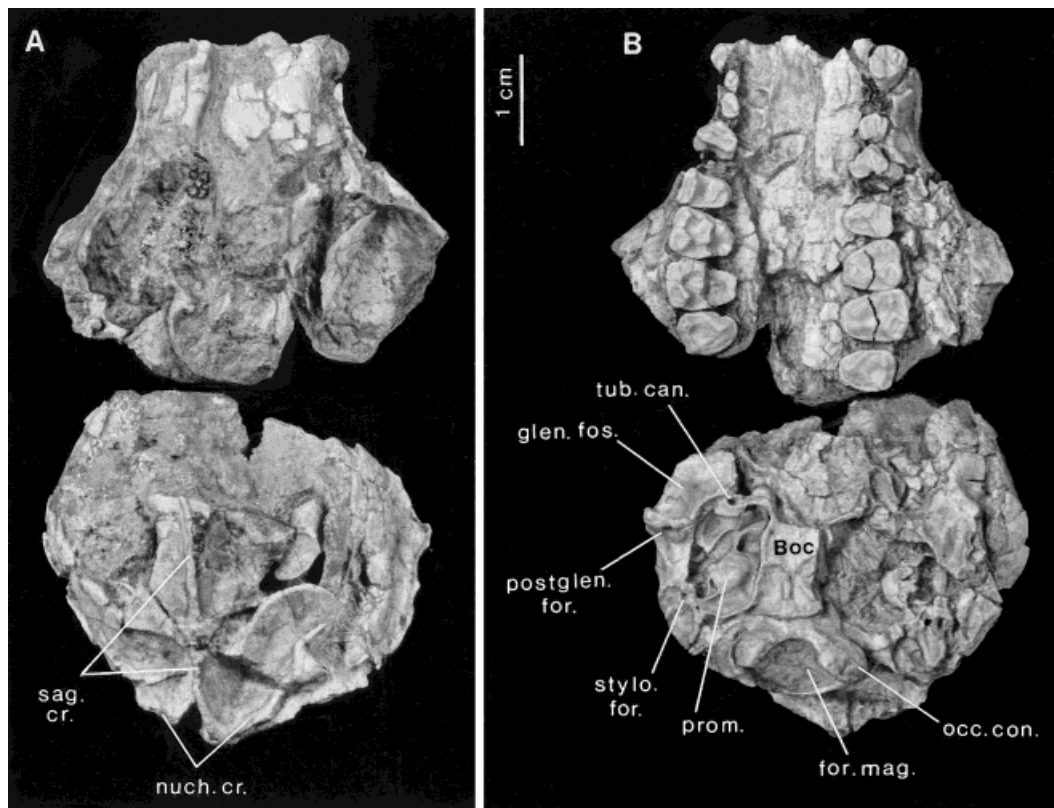


Fig. 3. Skull of *Cantius abditus*, USNM 494881, in dorsal (A) and ventral (B) view.

foramen magnum is larger in proportion to the occiput than in adapids.

The supraorbital process of the left frontal in *C. abditus*, though badly crushed, appears to be broad and long, as in the frontals of other notharctids. The orbits in USNM 494881 were evidently relatively large, although little more can be said on this point because the lateral portions of the eye sockets are missing.

The maxillae of USNM 494881 contain nearly complete P^3 – M^3 on both sides, as well as roots of right C and P^{1-2} and left C and P^2 (see Table 2 for measurements). They conform in all regards to known samples of *Cantius abditus* (Gingerich and Simons, 1977; O'Leary, 1996).

Discussion. The cranium displays several characters that are probably plesiomorphic for Notharctidae. These include the ventrally keeled basioccipital, flat basisphe-

noid, and proximally broad nasals. The latter character is also shared with adapids, and therefore is probably primitive for Adapiformes.

Auditory region of *Cantius*

Description. The ear region of USNM 494881 (Fig. 4) is the first one known that indisputably represents *Cantius*; it is also the oldest known adapiform auditory region. The following description is based primarily on the better-preserved right middle ear.

The ectotympanic is not preserved, and the bullar wall is too crushed to determine whether sutures were present. However, conditions in other adapiforms suggest that, by analogy, *Cantius* possessed an aphaneric, ringlike ectotympanic enclosed by a petrosal bulla (MacPhee, 1981).

The size and disposition of middle ear features and spaces are closely comparable to those of other adapiforms, such as *Notharctus*,

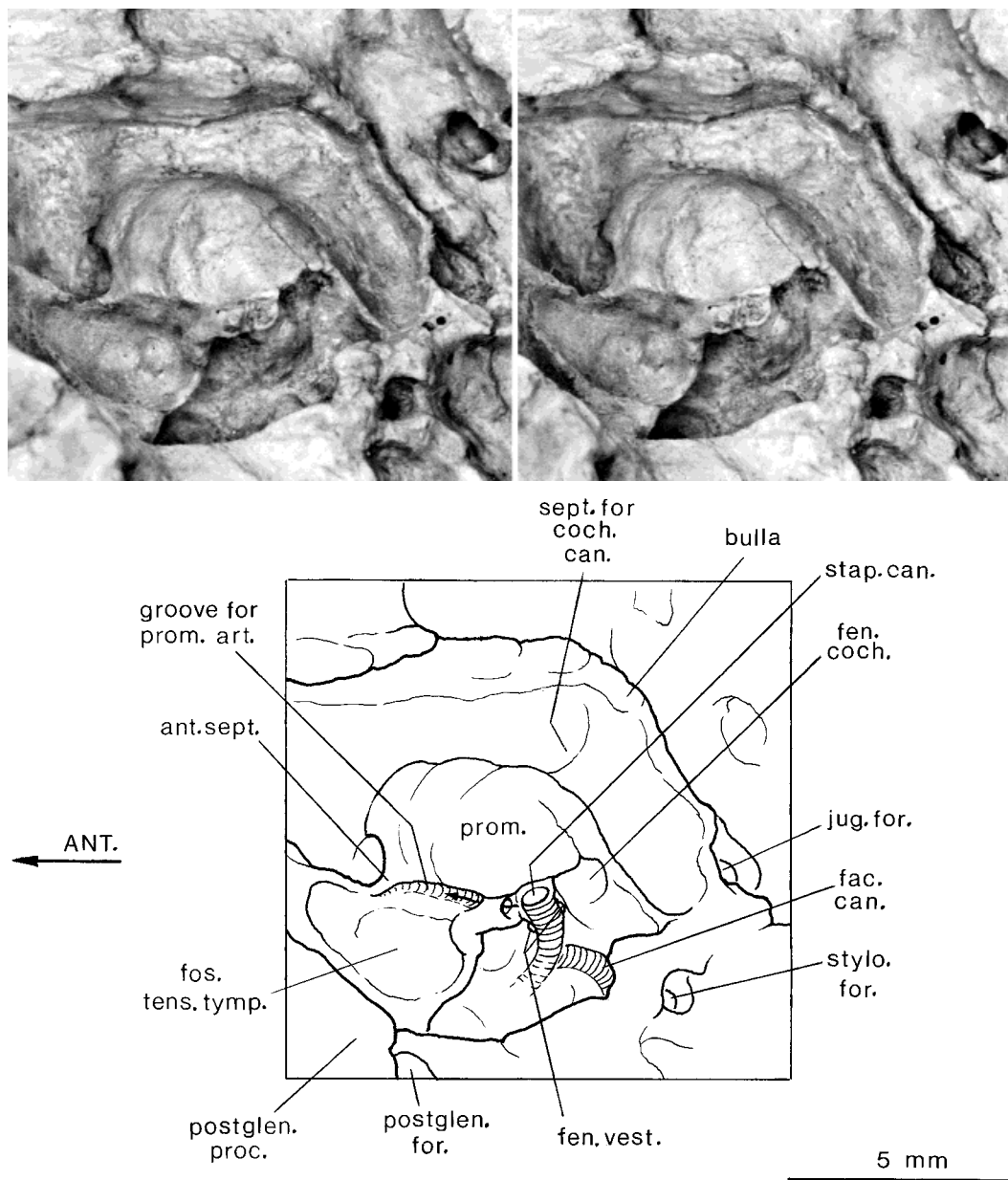


Fig. 4. Right middle ear of *Cantius abditus*, USNM 494881, stereopair, with interpretive drawing of same. Preserved bony features indicate that the promontorial artery was almost entirely unenclosed; a narrow bridge covered it for a short distance (arrow) just distal to its

anatomical origin from the internal carotid (canal not preserved). Thereafter, the vessel travelled in a shallow sulcus until it passed into the endocranium (not seen here due to matrix). Distal tracks of the stapedia artery and facial canal are obscured by matrix.

as well as modern lemurs (for details of which see MacPhee and Cartmill, 1986). Similarities extend to minor details such as the size and disposition of major and minor septa, the fossa

for the origin of *m. tensor tympani*, and the conformation of the area posterior to the fenestra cochleae. The better-preserved right auditory region has been distorted by crushing so

that the ostium for the tubal canal opens ventrally rather than directly rostrally.

Details of carotid circulation are highly significant for primate systematics (MacPhee and Cartmill, 1986), and for this reason we will concentrate on describing this aspect of the ear region of *Cantius abditus*. On the better-preserved right side, a large broken canal is seen on the posterolateral side of the promontorium, crossing the position of the fenestra vestibuli (Fig. 4). Immediately anterolateral to the canal there is a small bony eminence from which emerges a faint groove that traverses the lateral aspect of the promontorium. Comparison of these structures with conditions in noncheiropogonid lemurs (cf. illustrations in Gregory, 1920) indicates that the canal is the stapedia canal and the groove is the sulcus for the promontorial artery. Because the sulcus for the promontorial artery lacks defined walls, its width cannot be accurately measured on the skull of *C. abditus*. However, a vessel filling this sulcus can be estimated to have had a diameter about one-third to one-quarter that of the stapedia artery. (This does not entirely settle the matter, however, because by analogy to living lemurs the promontorial sulcus also carried nerves.) The small bony eminence attached to the stapedia canal is best interpreted as an enclosure for the proximal-most part of the promontorial artery, which was otherwise uncovered. The eminence extends as a rounded projection into the roof of the tympanic cavity (Fig. 4). However, inasmuch as the stapedia artery is already accounted for, the rounded projection cannot be for that vessel. As there are no known homologues of the intratympanic part of the stapedia ramus inferior in any primate (MacPhee and Cartmill, 1986), we prefer to interpret the projection as part of the wall of the epitympanic recess.

Discussion. With these features and identifications in mind, we may now compare *Cantius* to other adapiform primates. For two characters of the internal carotid circulation, *Cantius* is almost precisely like extant noncheiropogonid lemurs and differs from other known adapiforms:

- 1) Bony markings are consistent with the interpretation that the internal carotid divided into a large stapedia artery and a much smaller promontorial artery. This is similar to the arterial pattern present in two isolated primate petrosals (AMNH 88801 and 88802; Fig. 5) from East Alheit Pocket (Early Eocene Four Mile Fauna), which were referred to *?Pelycodus* by Szalay (1975). Assuming they are adapiform, which is probable judging from their size and anatomy, these petrosals must represent *Cantius ralstoni* (formerly placed in *Pelycodus*), the only adapiform primate known from that locality. On the basis of these specimens, Szalay (1975) argued that it might be primitive for adapiforms to have small promontorial arteries. Although these specimens are badly battered, it is reasonably clear that the intact stapedia canal had to have been significantly larger than the channel that carried the promontorial artery (as discussed below, whether the latter was a complete tube or merely a sulcus cannot be determined in this material). Other adapiforms in which arterial canals are intact enough for comparison show either subequal canals or a larger promontorial canal (MacPhee and Cartmill, 1986; Gunnell, 1995).
- 2) The promontorial artery evidently emerged onto the ventral surface of the promontorium and travelled into the endocranium along an open sulcus directed toward the ostium of the auditory tube. In the best-preserved adapiform basicranial material, all of which is notharctid (e.g., *Notharctus*, *Smilodectes*), the promontorial artery is completely enclosed in a canal from its morphological origin to the point at which it passes through a hiatus into the endocranium. In modern lemurs that possess intact internal carotid systems, such as *Eulemur* and *Lepilemur*, ossification of the canal tends to be less complete, and the artery's track across the promontorium is mostly unenclosed by bone. Some notion of the variation found in extant lemurs can be gained by examining the schematic drawings of Szalay and Katz (1973) (see also Conroy and Wible, 1978). There are few known

cranial specimens of adapids (e.g., *Lept-adapis*) with well-preserved basicrania, and the range of variation in this group remains unclear. MacPhee and Cartmill (1986), who personally examined cranial material of *Adapis parisiensis*, found that promontorial canals were distally incomplete in that species. Whether that condition obtains in "adapines" (adapids of this study) generally, as they inferred, seems probable but has not been adequately confirmed.

An additional important consideration is that canals within the middle ear are delicate structures and are easily destroyed by natural processes or during preparation. One of the Four Mile petrosals referred to *Cantius* (AMNH 88801, Fig. 5A) has only a groove for the stapedial artery, but by analogy with all other adapiforms it must originally have had a tube. Presumably the bony tube was broken away and its edges abraded to the extent that the initial presence of a tube has become ambiguous. The same situation cannot be excluded with respect to the promontorial groove in *Cantius*, as it could be argued that the eminence on the promontorium described above could be a fragment of a once-complete canal. This also applies to the promontorial groove in "*Hesperolemur*" (see below).

Nevertheless, if we are correct in inferring that the promontorial artery of *Cantius* was not enclosed in a tube, what might such evidence mean? One possibility is to assume, *vide* Szalay, that the most primitive arrangement of the internal carotid system resembled that of the majority of extant lemurs. *Cantius* would then be primitive, and adapiforms with complete canals and larger promontorial arteries would be derived for these features (and ?convergent on *Eosimias* and known omomyids except for *Shoshonius*, which also possess these traits; MacPhee et al., 1995). Alternatively, *Cantius* could be interpreted as displaying advanced carotid features, homologously shared with Lemuriformes (consequently, Adapiformes and Notharctidae would be paraphyletic). The teeth of *Cantius* obviously ally it with other adapiforms, suggesting that from the standpoint of character

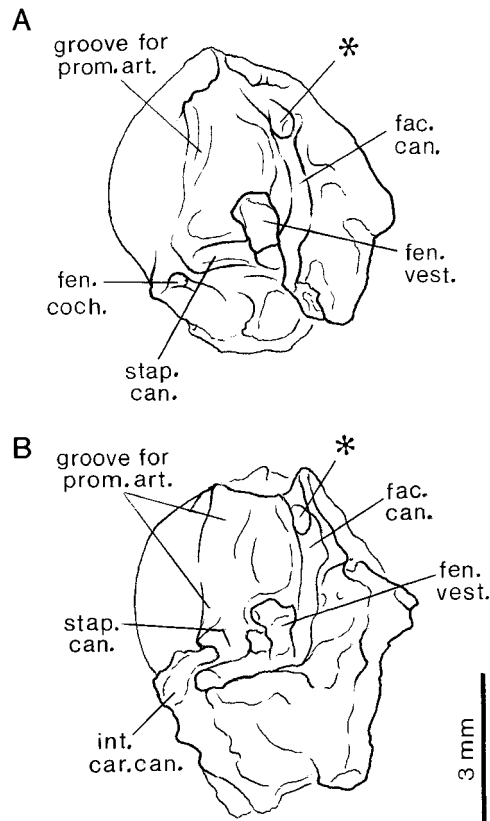


Fig. 5.

consistency, Szalay's hypothesis is probably correct: *Cantius* displays the primitive adapiform condition (quite possibly primitive for Adapiformes + noncheriogaleid lemurs as well).

REASSESSMENT OF "*HESPEROLEMUR*" *ACTIUS*

Gunnell (1995) recently described *Hesperolemur actius* as a new genus and species of notharctid. The hypodigm of this species consists of the holotype (a partial skull, SDSNH 35233, Figs. 6, 7), a right M_3 , and a broken left M_{27} , all from the early Uintan (Middle Eocene) of San Diego County, southern California. The skull is substantially complete posterior to the facial region but is crushed and distorted, as Gunnell noted. Although in most respects his description of the skull is accurate, in a few important ways it is not. These seriously affect both

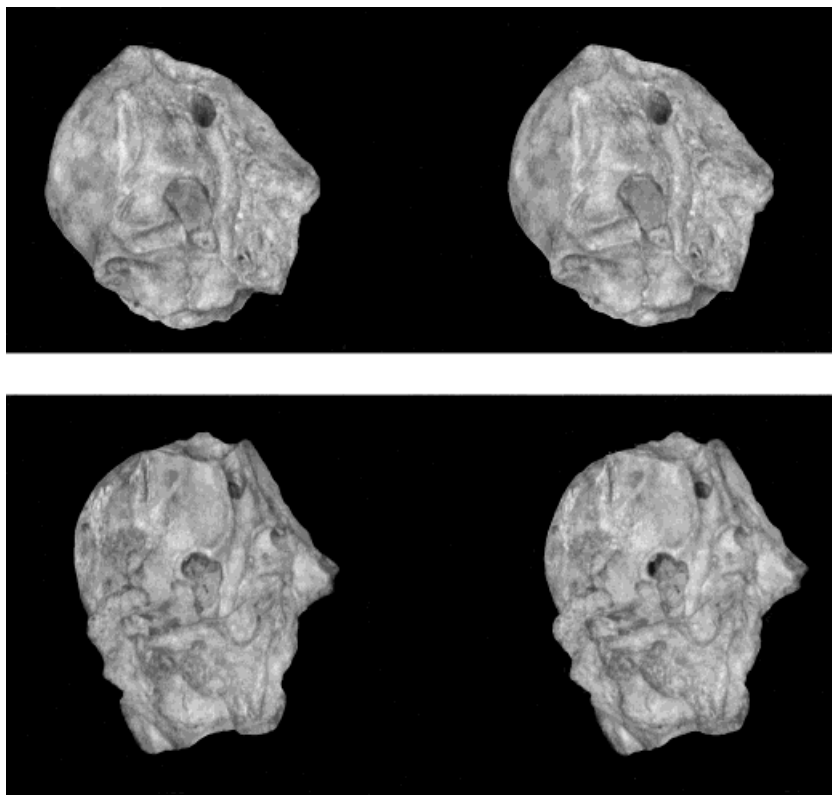


Fig. 5. Isolated left petrosals referred to *Cantius ralstoni*, AMNH 88801 (A) and AMNH 88802 (B); stereopairs, with interpretive drawings on facing page. AMNH 88802, formerly referred to *?Pelycodus* sp., was illustrated and described by Szalay (1975, Figs. 6 and 7). Asterisk indicates position of geniculum of facial nerve, ventral to which the tympanic part of the facial nerve enters the middle ear cavity.

morphological interpretation and systematic determination.

In particular, it is necessary to point out that the specimen's left side (Fig. 7B), which is the source of most of the basicranial characters discussed by Gunnell (1995), is very severely damaged, so severely that nothing remains of the cochlear housing on this side. The area that Gunnell believed to be the surface of the promontory actually consists of portions of the bony labyrinth of the inner ear exposed by random breakage.

In making morphological interpretations of incomplete specimens, it is often helpful to inspect fossils that are broken in similar (but not identical) ways. This can be appreciated by examining Figure 7C, which depicts a broken specimen of the left ear region of *Notharctus tenebrosus* (AMNH 11466). In this specimen the cochlear housing has also

spalled off, but the damage is less than in the "*Hesperolemur*" holotype. Here it is quite evident that a section of the osseous spiral lamina is exposed, encircled by the broken line of the cochlear housing. It is this lamina, with its vaguely canal-like aspect, that is exposed in the left auditory region of "*Hesperolemur*" and was identified by Gunnell (1995) as the "groove for promontory branch of internal carotid artery." Other features are similarly misidentified (see legend, Fig. 7).

The dentition of "*Hesperolemur*" is incompletely known in the holotype, and only two isolated teeth (lower molars that are neither associated nor directly comparable with the holotype) have been referred to this taxon. All of the teeth in question are either worn or damaged. Gunnell (1995) noted several minor differences between these teeth and those of other notharctids, the most signifi-

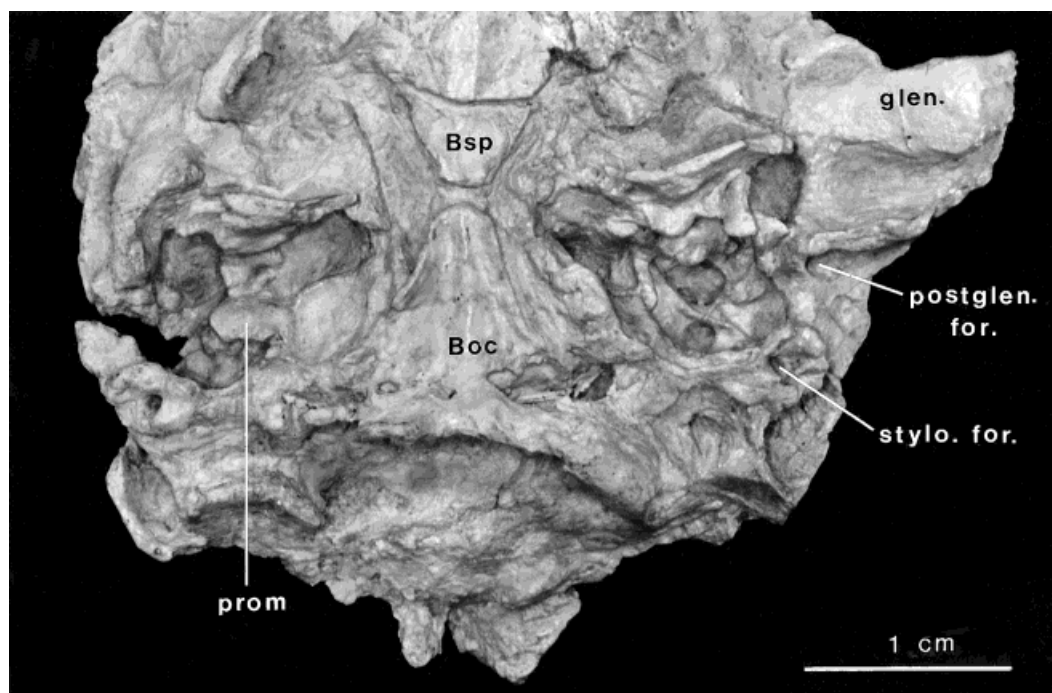


Fig 6. General view of posterior basicranium of "*Hesperolemur*" *actius*, SDSNH 35233. See Fig. 7A-B for enlargements of auditory region.

cant apparently being an inflated metaconid and the absence of a paraconid on the lower molars. Inspection of *Cantius* specimens in the USGS collection indicates that primitive species tend to have distinct paraconids, but in more derived species, such as *C. abditus*, the paraconid is typically very small and closely appressed to the much larger metaconid on M_{2-3} . Occasionally the paraconid is absent on M_3 , but no specimens were observed that lack a paraconid on M_2 . Therefore, absence of an M_2 paraconid alone seems insufficient basis for generic distinction. Gunnell (1995) observed that the upper teeth of "*Hesperolemur*" differ from those of *Notharctus* in having a weaker mesostyle and hypocone, and a narrower styler shelf. These are similarities to *Cantius*. Thus "*Hesperolemur*" *actius* appears to differ dentally from Wasatchian *Cantius* species to about the extent that *Cantius* species differ from each other. In our judgment, the dental characters initially cited as distinguishing features of "*Hesperolemur*" do not warrant erection of a new genus-level taxon.

Indeed, as Gunnell (1995) emphasized, the distinctiveness of "*Hesperolemur*" rests almost entirely on certain characters he detected in the ear region of the holotype. According to Gunnell, "*Hesperolemur*" diagnostically differs from all other adapiforms in that 1) the anterior crus of the ectotympanic is fused to the internal surface of the lateral bullar wall, and 2) the intratympanic divisions of the internal carotid artery lack bony canals. Also, he provisionally concluded that 3) the stapedial artery may be absent, which would be another difference from other adapiforms (and most other nonanthropoid primates).

Our restudy of the holotype (Figs. 6, 7) indicates that both ear regions are so damaged that few facts about their morphological organization can be stated with certainty. Nevertheless, even when due allowance is made for differing interpretations of ambiguous or poorly preserved structures, we find that Gunnell's (1995) interpretation of the distinctiveness of "*Hesperolemur*" cannot be sustained. (Features

that are otherwise not referenced here, such as the borders of the auditory bulla, transit of the facial nerve, and various foramina identified by Gunnell (1995), are accurately described by him in the original publication and do not require additional comment, other than to point out that they strongly underline the notharctid affinities of "*Hesperolemur*."

With respect to the first character, Gunnell (1995, p. 456) correctly stated that the anterior third of the anulus of SDSNH 35233 (all that is preserved of either ectotympanic in this specimen) is "solidly fused to the internal bullar wall." However, he went on to say that contact is achieved by means of an annular bridge, "petrosal in origin," and that this feature is separated from the ectotympanic proper by a small gap equivalent to the recessus dehiscence (i.e., the gap between the ectotympanic proper and the petrosal bulla in adapiforms and most lemurs; see MacPhee and Cartmill, 1986). Our observations are somewhat different. The fragmentary apex of the anterior crus of the ectotympanic is solidly attached to the internal bullar wall, but the small piece preserved displays no evidence of either a petrosal-derived annular bridge or a recessus dehiscence. (Nor would either feature be expected so close to the crural apex in any adapiform or lemur; cf. MacPhee, 1981.) In fact, the line drawing by Gunnell (1995, Fig. 4) of the left ear region shows that the structure labelled "EC" is integral, and in our view is comprised of ectotympanic material exclusively.

In these respects the position of the crural apex of the ectotympanic on the internal bullar wall in "*Hesperolemur*" is unexceptional. In all investigated adapiforms and lemurs other than large subfossil species (MacPhee, 1987), the crural apex is appressed to the petrosal bulla (or more accurately, the roof of the tympanic cavity). The only notable difference is that in extant small-bodied lemurs the two bones are not, or are only very lightly, fused, whereas fusion appears to be general in investigated adapiforms (MacPhee, 1981; MacPhee and Cartmill, 1986).

Although Gunnell (1995) wondered parenthetically whether the ectotympanic of "*Hes-*

perolemur" might have contacted the petrosal plate along its entire arc (as it does, for example, in lorises), no specific type of ectotympanic-petrosal relationship (cf. MacPhee, 1981) can be inferred from crural-petrosal contact alone, since contact occurs in all primates of modern aspect.

With respect to the second character, the enclosure and patterning of the intratympanic internal carotid system, we find that the only vascular impression unequivocally present in the holotype's middle ear is a small portion of the channel for the promontorial artery, on the specimen's right side only (Fig. 7A). All that remains of this feature, however, is a relatively deep, U-shaped channel. Whether a bony tube enclosed the artery or not cannot be determined (see above).

Although it has been claimed that adapiforms characteristically differ from omomyids in presenting a large stapedial and smaller promontorial artery (cf. Szalay, 1975, 1977), as in the *Cantius* skull described above, in fact there is significant variation within both notharctids and adapids (MacPhee and Cartmill, 1986). Gunnell (1995) provided additional evidence for such variation. While there is no direct evidence of stapedial caliber in "*Hesperolemur*," by comparison with other adapiforms of similar body size the right promontorial groove is unquestionably large, as, presumably, was the artery that it conducted. Its size is comparable to that in *Notharctus* and *Smilodectes* and apparently relatively larger than in *Cantius abditus*.

As noted above, Gunnell (1995) identified a channel for the promontorial artery on the skull's left side (Fig. 7B), which we interpret as a section of the osseous spiral lamina, exposed by breakage. A specimen of *Notharctus tenebrosus*, similarly broken, is illustrated for comparison in Figure 7C.

Despite the cautious inference by Gunnell (1995) that the stapedial artery may have been absent, in our judgment nothing can be concluded about the condition of this vessel because the lateral parts of the middle ear (as here reinterpreted) are either missing or badly damaged on both sides. Thus we can say nothing about the size of the promontorial artery relative to the stapedial artery.

What can be said about the relative derivedness of the ear region of "*Hesperolemur*"? Considering only characters that can be reliably inferred from preserved morphology, there is no demonstrable difference from other adapiforms except in one important regard: if Gunnell's (1995) interpretation is correct, the promontorial artery was evidently not enclosed in a bony tube. This is a potential difference from all other adapiforms except *Cantius abditus*, and is similar to the condition seen to a greater or lesser extent in the auditory regions of extant lemurs (Szalay and Katz, 1973). Whether there was a canal around the internal carotid stem in SDSNH 35233 cannot be determined because all structures related to the passage of that vessel have been lost. (It is parsimonious to infer that the artery itself was present, because there is no known case within primates in which the promontorial artery is large and functional but the internal carotid stem is absent. Parsimony does not permit a similar inference in the case of the stapedial artery, absent in some haplorhine clades.)

SUMMARY AND CONCLUSIONS

A new specimen of *Cantius abditus*, the most complete skull and mandible of *Cantius* known, provides evidence of the anterior dentition and basicranial anatomy. It has strongly inclined lower incisors with spatulate crowns, I_2 larger than I_1 , and large, projecting canines. Canine size, and incisor proportions and morphology, but not orientation, closely resemble conditions in some primitive anthropoids (e.g., *Catopithecus*, but not *Eosimias*); but somewhat similar conditions are also known in some omomyids, raising doubt as to their significance for adapiform-anthropoid relationship. Incisor orientation might alternatively be interpreted as a synapomorphy with tooth-combed prosimians (which might already have been in existence by the Early Eocene; Yoder et al., 1996), but canine and incisor crown morphology differs. It is also possible that the degree of incisor inclination was primitive for euprimates. Other dental contrasts with either or both groups could also represent euprimate symplesiomorphies.

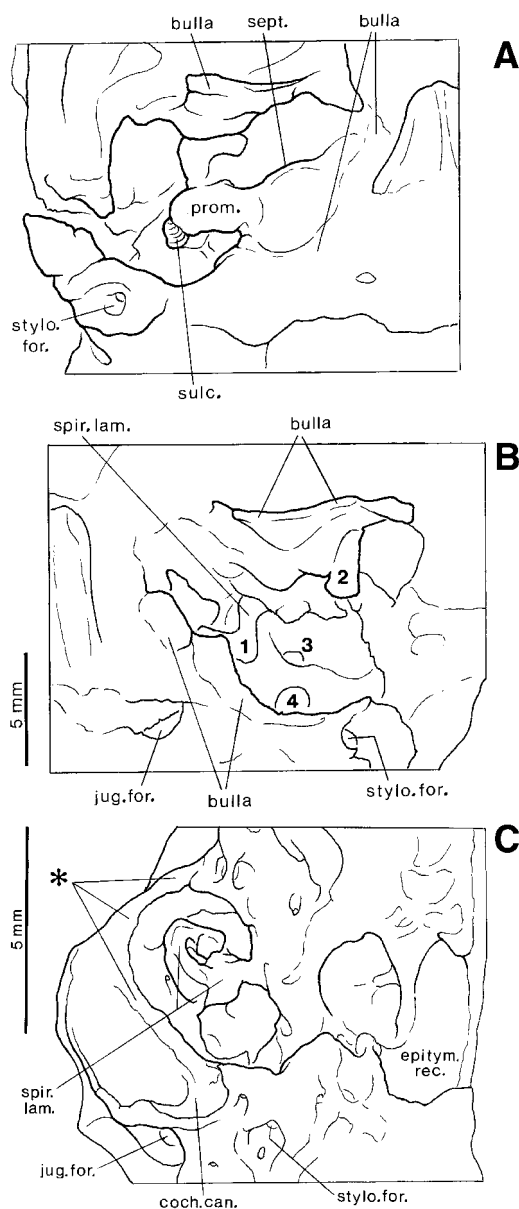


Fig 7.

The auditory region of *Cantius* differs from that of other notharctids and corresponds closely with extant noncheirolepid lemurs in showing a large (enclosed) stapedial artery and a much smaller promontorial artery apparently situated in an unenclosed sulcus. These conditions are interpreted as primitive for Adapiformes rather than indica-

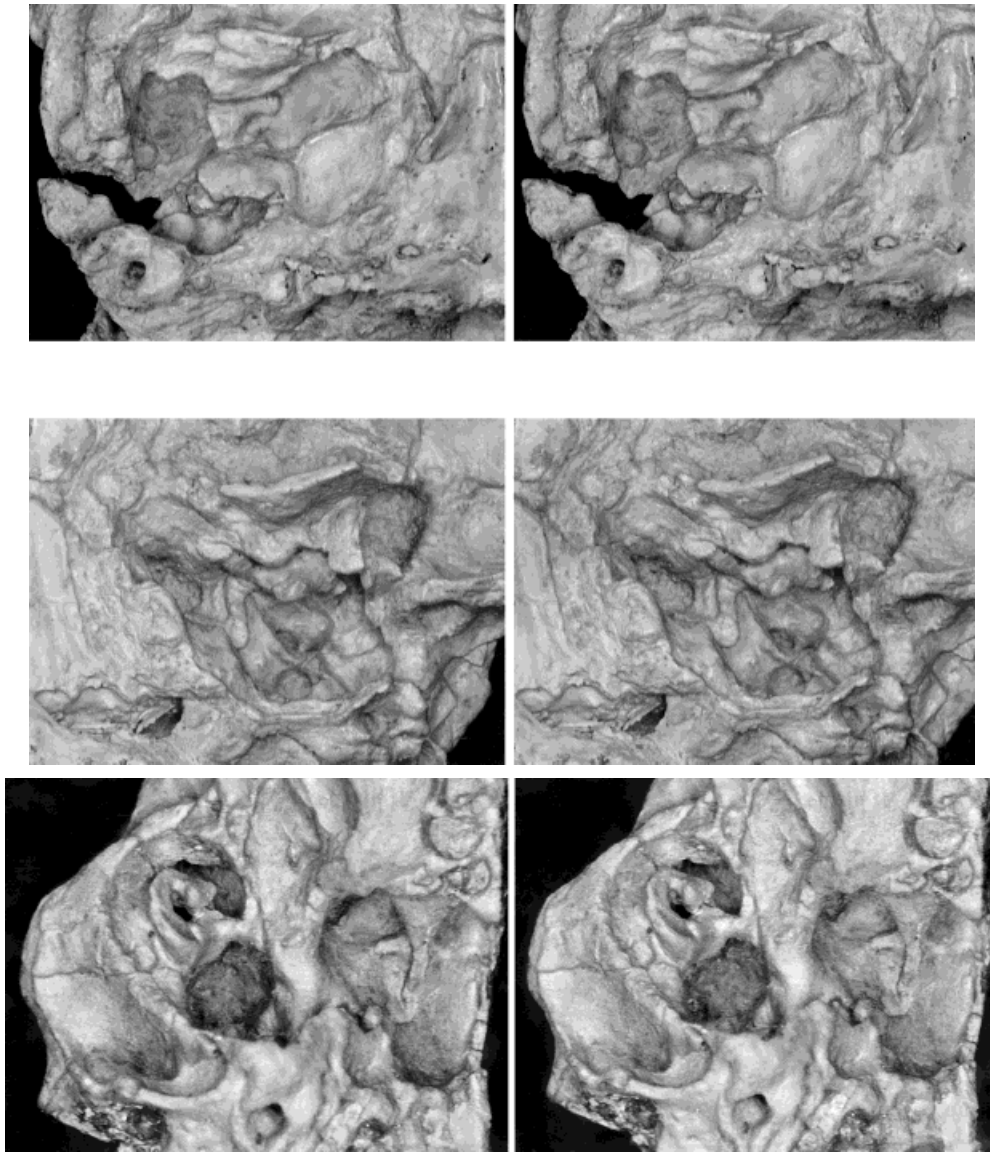


Fig. 7. Closeups of right (A) and left (B) auditory regions of *Hesperolemur* *actius*, SDSNH 35233. C: Damaged left auditory region of *Northarctus tenebrosus* (AMNH 11466), showing exposure of inner ear similar to condition of SDSNH 35233. All are stereopairs, with interpretive drawings on facing page. In *Hesperolemur* holotype, cochlear housings (promontoria) are broken on both sides, although the right side is slightly better preserved. Bullae are represented only by fragments. In A, "sulic," a troughlike feature on the deficient lateral aspect of the promontory, is interpreted as the track of the promontorial artery. Numbered features in B correlate with features identified in Gunnell's (1995) original

figure 4; structures are reinterpreted as follows. Features 1, originally labelled "PC" (groove for promontory branch of internal carotid artery), is a remnant of the osseous spiral lamina. Feature 2, originally labelled "EC" (ectotympanic), is certainly ectotympanic, but with no evidence of an annular bridge. Feature 3, originally labelled "VF" (vestibular fenestra), is the intracochlear aspect of the internal acoustic meatus. Feature 4, originally labelled "CF" (cochlear fenestra), may be part of the vestibule of the bony labyrinth, but the condition of the specimen precludes definite identification. The asterisk in C indicates the broken edge of the cochlear housing.

tive of special relationship between *Cantius* and noncheirogaleid lemurs. Together with the dental evidence, they suggest that *Cantius* closely approached the euprimate morphotype.

Restudy of the damaged basicranium of "*Hesperolemur*" *actius* leads to the conclusion that no fundamental difference from other notharctids can be demonstrated. Its only remarkable feature, the presence of a possibly unenclosed promontorial artery, is a potential resemblance to *Cantius*. Although the apparently large size of the promontorial artery is more suggestive of *Notharctus* than of *Cantius*, documented variability in artery caliber indicates that this is not a very useful taxonomic character of adapiforms. Characters of the dentition help to clarify the position of "*Hesperolemur*" among notharctids. Dental differences cited by Gunnell (1995) make it unlikely that "*Hesperolemur*" and *Copelemur* are congeneric, though the cranial features of *Copelemur*, which could shed light on this possibility, are unknown. The presence of mesostyles in "*Hesperolemur*" *actius* excludes it from *Pelycodus*, and the relatively weak development of the mesostyles and hypocone diminishes the likelihood that it represents *Notharctus* or *Smilodectes*. These same features, however, make it very difficult to distinguish from *Cantius*. Although the holotype of "*Hesperolemur*" *actius* is geographically and temporally separated from known species of *Cantius*, morphologically it is insufficiently distinct from the latter to warrant separation under a different genus. Dental characters, however, support its recognition as a valid species, *Cantius actius*.

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